

General Characters of fungi - Definition of fungus, somatic structures, types of fungal thalli, fungal tissues, modifications of thallus, reproduction in fungi (asexual and sexual)

General characters of fungi

Fungi are the eukaryotic, achlorophyllous, and unicellular or multicellular organisms, which may reproduce by asexual and sexual spores.

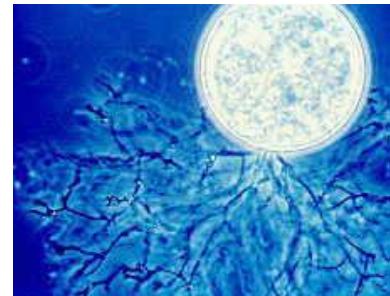
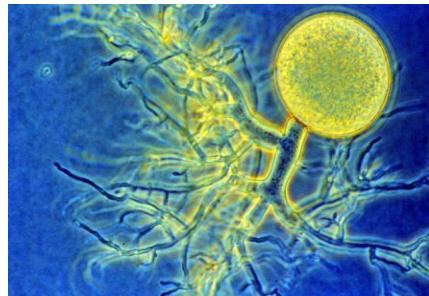
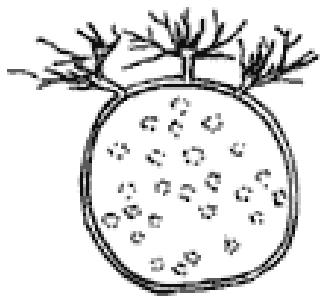
1. All are eukaryotic - Possess membrane-bound nuclei (containing chromosomes) and a range of membrane-bound cytoplasmic organelles (e.g. mitochondria, vacuoles, endoplasmic reticulum).
2. Most are filamentous - Composed of individual microscopic filaments called hyphae, which exhibit apical growth and which branch to form a network of hyphae called a mycelium.
3. Some are unicellular - e.g. yeasts.
4. Protoplasm of a hypha or cell is surrounded by a rigid wall - Composed primarily of chitin and glucans, although the walls of some species contain cellulose.
5. Many reproduce both sexually and asexually - Both sexual and asexual reproduction often result in the production of spores.
6. Their nuclei are typically haploid and hyphal compartments are often multinucleate - Although the oomycota and some yeast possess diploid nuclei.
7. All are achlorophyllous - They lack chlorophyll pigments and are incapable of photosynthesis.
8. All are chemoheterotrophic (chemo-organotrophic) - They utilise pre-existing organic sources of carbon in their environment and the energy from chemical reactions to synthesize the organic compounds they require for growth and energy.
9. Possess characteristic range of storage compounds - e.g. trehalose, glycogen, sugar alcohols and lipids.
10. May be free-living or may form intimate relationships with other organisms i.e. may be free-living, parasitic or mutualistic (symbiotic).

Thallus

The body of the fungus is called as 'thallus'.

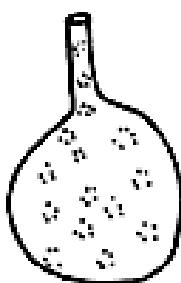
Eucarpic thallus

The thallus is differentiated into vegetative part, which absorbs nutrients, and a reproductive part, which forms reproductive structure. Such thalli are called as eucarpic. e.g. *Pythium aphanidermatum*.



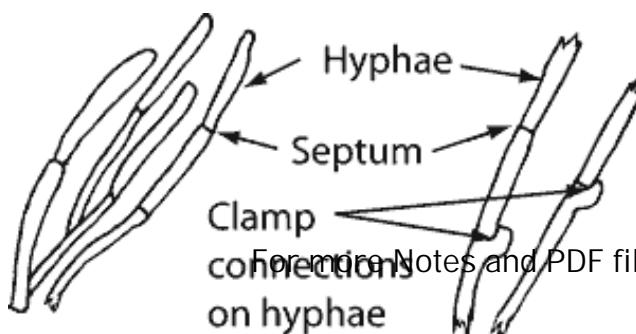
Holocarpic thallus

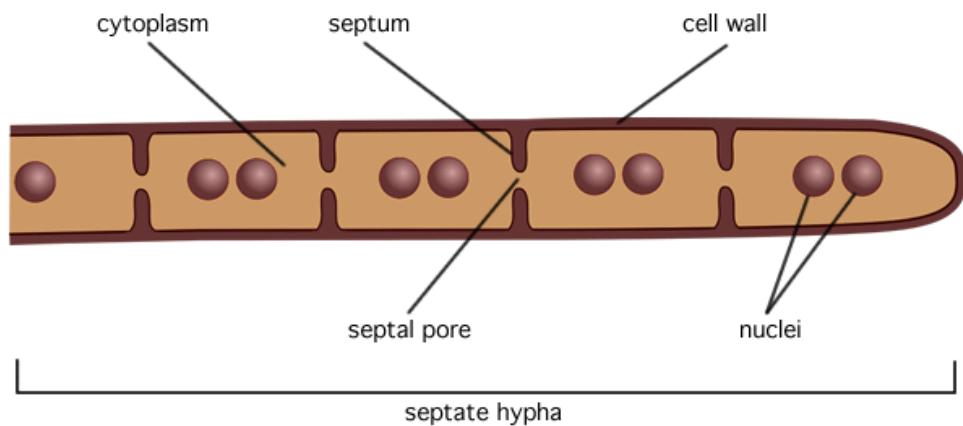
The thallus does not show any differentiation on vegetative and reproductive structure. After a phase of vegetative growth, it gets converted into one or more reproductive structures. Such thalli are called as 'holocarpic' e.g. yeast, *Synchytrium endobioticum*



Hyphae

Hyphae is a tubular, transparent filament, usually branched, composed of an outer cell wall and a cavity (lumen) lined or filled with protoplasm including cytoplasm. Hyphae are divided into compartments or cells by cross walls called septa and are generally called as septate (with cross wall) or coenocytic (aseptate -without cross wall). Hyphae of most of the fungi measure 5-10 μm across.





Mycelium (pl. Mycelia)

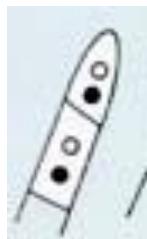
The hyphal mass or network of hyphae constituting the body (thallus) of the fungus is called as mycelium. The mycelium of parasitic fungi grows on the surface of the host and spread between the cells and it is called intercellular mycelium. The mycelium of parasitic fungi, which grows on the surface of the host and penetrates into the host cells and is called intracellular mycelium. If the mycelium is intercellular, food is absorbed through the host cell walls or membrane. If the mycelium penetrates into the cells, the hyphal walls come into direct contact with the host protoplasm. Intercellular hyphae of many fungi, especially of obligate parasites of plants (fungi causing downy mildews, powdery mildews and rusts) obtain nutrients through haustoria.

Monokaryotic mycelium (uninucleate)

Mycelium contains single nucleus that usually forms part of haplophase in the life cycle of fungi.

Dikaryotic mycelium (binucleate)

Mycelium contains pair of nuclei (dikaryon), which denotes the diplophase in the life cycle of fungi.



Homokaryotic mycelium

The mycelium contains genetically identical nuclei.

Heterokaryotic mycelium

The mycelium contains nuclei of different genetic constituents.

Multinucleate

The fungal cell contains more than 2 nuclei.

Septa

Transverse septa occur in the thallus of all filamentous fungi to cut off reproductive cells from the rest of the hypha, to separate off the damaged parts or to divide the hypha into regular or irregular compartments or cells. There are two general types of septa in fungi viz., primary and adventitious. The primary septa are formed in association with nuclear division and are laid down between daughter nuclei. The adventitious septa are formed independently of nuclear division and are especially associated with changes in the concentration of the protoplasm as it moves from one part of the hypha to another.



Transverse septa

Septa vary in their construction septa have biological importance in the lifecycle of fungi. Some are simple whereas others are complex. All types of septa are formed by centripetal growth from the hyphal wall inward. In some septa, the growth continues until the septum is a solid plate. In others the septum remains incomplete, leaving a pore in the centre that may often be plugged or occulted.

Some groups of Basidiomycetes like Auriculariaceae, Tremellaceae, Aphylophorales, Agaricales etc (except Ustilaginales and uredinales) have more complex septa. Surrounding the central pore in the septum is a curved flange of wall material, which is thickened to form a barrel-shaped or cylindrical structure surrounding the pore. Septa of this type are termed dolipore septa (L. *dolum* = a large jar or cask i . e., barrel).

These septa are often overlaid by perforated cap, which is an extension of the endoplasmic reticulum. This cap is known as parenthosome or pore cap. Despite these apparent barriers, there is a good cytoplasmic continuity between adjacent cells. The septal pore may vary in width from 0.1 to 0.2 μm . Dolipore septa are found in both monokaryotic and dikaryotic mycelia.

Fungal cell structure

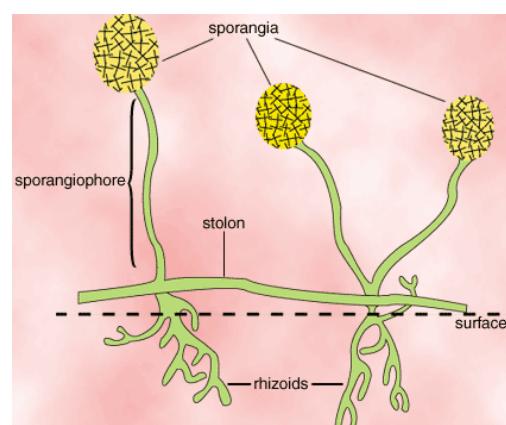
Fungal cells are typically eukaryotic and have distinguished characteristics than that of bacteria, and algae. The chief components of cell wall appears to be various types of carbohydrate or their mixtures (upto 80-90%) such as cellulose, pectose, callose etc., cellulose predominates in the cell wall of mastigomycotina (lower fungi) while in higher fungi chitin is present. The living protoplast of the fungal cell is enclosed in a cell membrane called as plasma membrane or plasmalemma. Cytoplasm contains organelles such as nucleus, mitochondria, Golgi apparatus, ribosomes, vacuoles, vesicles, microbodies, endoplasmic reticulum, lysosomes and microtubules.

The fungal nucleus has nuclear envelope comprising of two typical unit membrane and a central dense area known as nucleolus, which mainly consist of RNA. In multinucleate hyphae, the nuclei may be interconnected by the endoplasmic reticulum. Vacuoles present inside the cell provide turgor needed for cell growth and maintenance of cell shape. Beside the osmotic function, they also store reserve materials. The chief storage products of fungi are glycogen and lipid. The apex of the hyphae are usually rich in vesicles and are called as apical vesicular complex (AVC) which helps in the transportation of products formed by the secretary action of golgi apparatus to the site where these products are utilized.

Specialized Somatic Structures

Rhizoid

A rhizoid (Gr. *rhiza* = root + *oides* = like) is a short, root-like filamentous outgrowth of the thallus generally formed in tufts at the base of small unicellular thalli or small porophores. Rhizoid serves as anchoring or attachment organ to the substratum and also as an organ of absorption of nutrients from substratum. Rhizoids are short, delicate filaments that contain protoplasm but no nuclei.

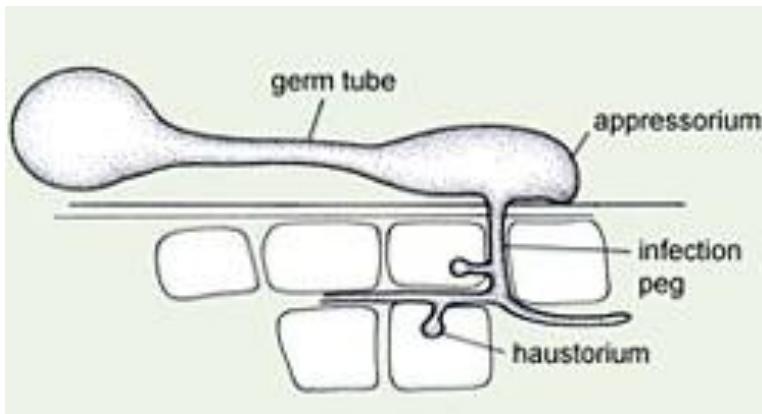


Rhizoids are common in lower fungi like Chytridiomycetes, Oomycetes and Zygomycetes. Some species produce a many-branched rhizomycelium. This is an extensive rhizoidal system that usually do not contain nuclei, but through which nuclei migrate. e.g.

Cladochytrium sp. On rhizomycelium numerous sporangia develop. Such thalli are polycentric, that is, they form several reproductive centres instead of a single one where the thallus is termed monocentric.

Appressorium

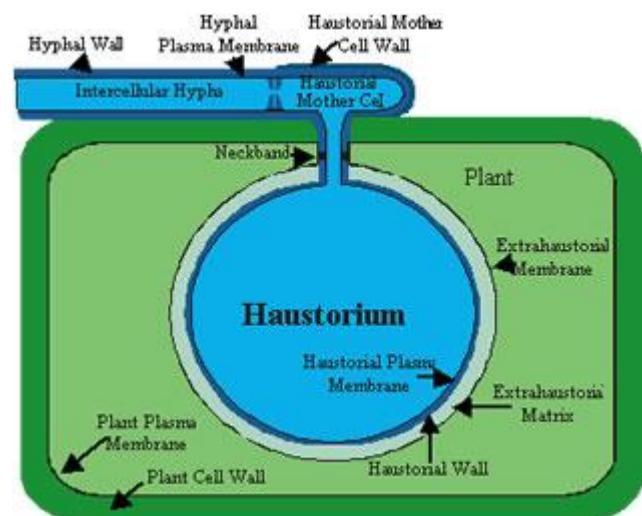
Appressorium (p1. appressorium; L. *apprimere* = to press against) is a simple or lobed structure of hyphal or germ tube and a pressing organ from which a minute infection peg usually grow and enter the epidermal cell of the host. It helps germ tube or hypha to attach to the surface of the host or substrates. These appressoria are formed from germ tubes of Uredinales (rust fungi), Erysiphales (powdery mildew fungi) and other fungi in their parasitic or saprophytic stages. In addition to giving anchorage, appressoria help the penetrating hyphae, branches to pierce the host cuticle. In fungi like *Colletotrichum falcatum*, germ tubes from conidia and resulting hyphae form appressoria on coming in contact with any hard surface like soil etc. These appressoria are thought to function as resting structures (chlamydospores) also.



Haustoria

Haustoria (sing. haustorium; L. *haustor* = drinker) are special hyphal structures or outgrowths of somatic hyphae sent into the cell to absorb nutrients. The hyphal branch said to function as haustorium becomes extremely thin and pointed while piercing the host cell wall and expands in the cell cavity to form a wider, simple or branched haustorium. Haustoria may be knob-like or balloon – like in shape, elongated or branched like a miniature root system. The hyphae of obligate parasites of plants like downy mildew, powdery mildew or rust fungi late blight fungus etc., produce haustoria. Hyphopodia: Hyphopodium (pl. hyphopodia Gr. *hyphe* = web + *pous* = foot) is a small appendage with one or two cells in length on an external hypha and function as absorbing structures. The terminal cell of hyphopodium is expanded and rounded or

pointed. Sometimes it produces a haustorium. e.g. Ectophytic fungi (*Meliola aesariae*) attacking leaves of green plants.



Aggregations of hyphae and tissues

a. Mycelial strand

Mycelial strands are aggregates of parallel or interwoven undifferentiated hyphae, which adhere closely and are frequently anastomosed or cemented together. They are relatively loose (e.g. *Sclerotium rolfsii* growth on culture medium) compared to rhizomorph. They have no well-defined apical meristem. Mycelial strand formation is quite common in Basidiomycetes, Ascomycetes and Deuteromycetes. Mycelial strands form the familiar 'spawn' of the cultivated mushroom, *Agaricus bisporus*. Mycelial strands are capable of translocating materials in both the directions. They are believed to afford means by which a fungus can extend an established food base and colonize a new substratum, by increasing the inoculum potential of the fungus at the point of colonization.

b. Rhizomorph

Rhizomorph (Gr. *rhiza*=root + *morphe* = shape) is the aggregation of highly differentiated hyphae with a well defined apical meristem, a central core of larger, thin walled, cells which are often darkly pigmented. These root-like aggregation is found in the honey fungus or honey agaric *Armillariella mellea* (= *Armillaria mellea*). They grow faster than the mycelial strands. The growing tip of rhizomorph resembles that of a root tip. The fungus may spread underground from one root system to another by means of rhizomorph.

c. Fungal tissues

During certain stages of the life cycle of most fungi, the mycelium becomes organized into loosely or compactly woven tissues. These organized fungal tissues are called plectenchyma (Gr. *plekein* = to weave + *encyma* = infusion i.e., a woven tissue). There are two types of plectenchyma viz., prosenchyma and pseudoparenchyma. When the tissue is loosely woven and the hyphae lie parallel to one another it is called prosenchyma (Gr. *pros* = toward + *enchyma* = infusion, i.e., approaching a tissue). These tissues have distinguishable and typical elongated cells. Pseudoparenchyma (Gr. *Pseudo* = false) consists of closely packed, more or less isodiametric or oval cells resembling the parenchyma cells of vascular plants. In this type of tissues hyphae lose their individuality and are not distinguishable. Cells in prosenchyma are thin-walled and cells in pseudoparenchyma.

Stroma and sclerotium

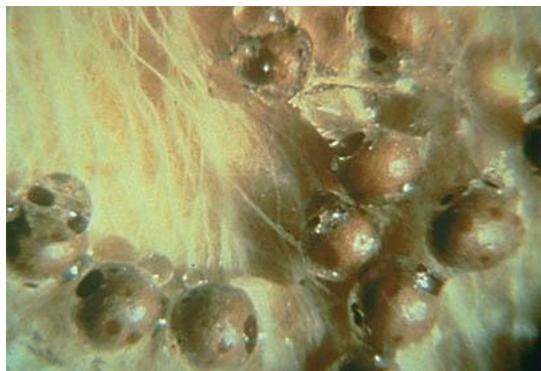
Stromata and sclerotia are somatic structures of fungi.

i. **Stroma** (pl. stromata; Gr. *stroma* = mattress)

A stroma is a compact, somatic structure or hyphal aggregation similar to a mattress or a cushion, on which or in which fructifications of fungi are usually formed. They may be of various shapes and sizes. Hyphal masses like acervuli, sporodochia, pionnotes etc. are the fertile stromata, which bear sporophores producing spores.

ii. **Sclerotium** (pl. sclerotia; Gr. *skeleros* = hard)

A sclerotium is a resting body formed by aggregation of somatic hyphae into dense, rounded, flattened, elongated or horn-shaped dark masses. They are thick-walled resting structures, which contain food reserves. Sclerotia are hard structures resistant to unfavourable physical and chemical conditions. They may remain dormant for longer periods of time, sometimes for several years and germinate on the return of favourable conditions. The sclerotia on germination may be myceliogenous and produce directly the mycelium e.g. *Sclerotium rolfsii*, *Rhizoctonia solani* and *S. cepivorum* (white rot of onion).



They may be sporogenous and bear mass of spores. e.g. *Botrytis cinerea*. They may also be carpogenous where in they produce a spore fruit (ascocarps or basidiocarps) bearing stalk. e.g. *Sclerotinia* sp. *Claviceps purpurea* (ergot of rye). Development of ascocarps is seen in *Sclerotinia*, where stalked cups or apothecia, bearing asci, arise from sclerotia. In *Claviceps purpurea*, sclerotia germinate and give rise to drumstick like structures called perithecial stromata, which contain perithecia, flask-shaped cavities within which the asci are formed.

Mycorrhizae

Mycorrhiza (pl. mycorrhizae; Gr. *mykes* = mushroom + *rhiza* = root) is the symbiotic association between higher plant roots and fungal mycelia. Many plants in nature have mycorrhizal associations. Mycorrhizal plants increase the surface area of the root system for better absorption of nutrients from soil especially when the soils are deficient in phosphorus.

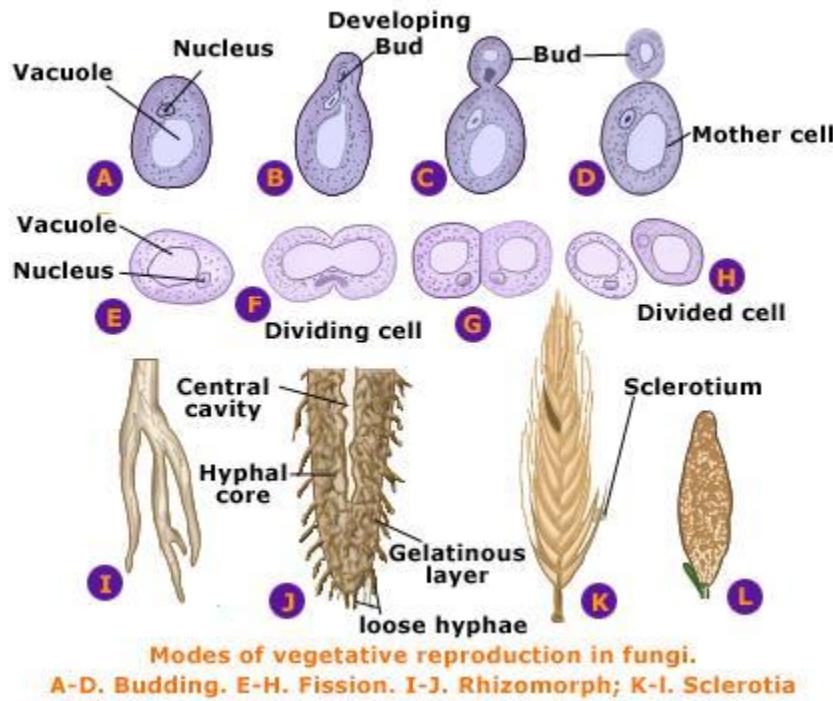
The nature of association is believed to be symbiotic (mutualism), non-pathogenic or weakly pathogenic. There are three types of mycorrhizal fungal associations with plant roots. They are ectotrophic or sheathing or ectomycorrhiza, endotrophic or endomycorrhiza and ectendotrophicmycorrhiza.

REPRODUCTION

Reproduction is the formation of new individuals having all the characteristics typical of a species. The fungi reproduce by means of asexual and sexual or parasexual reproduction. Asexual reproduction is sometimes called somatic or vegetative and it does not involve union of nuclei, sex cells or sex organs. The union of two nuclei characterizes sexual reproduction.

ASEXUAL REPRODUCTION

In fungi, asexual reproduction is more important for the propagation of species. Asexual reproduction does not involve union of sex organs (gametangia) or sex cells (gametes) or nuclei. In fungi the following are the common methods of asexual reproduction.



1. Fragmentation of mycelium

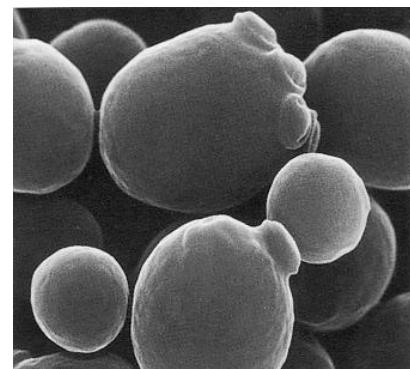
Mycelial fragments from any part of the thallus may grow into new individuals when suitable conditions are provided.

2. Fission of unicellular thalli

It is also known as transverse cell division. Reproduction by the method of fission is observed in fungi. Fission is simple splitting of cells into two daughter cells by constriction and the formation of a cell wall. It is observed in *Schizosaccharomyces* spp.

3. Budding

Budding is the production of a small outgrowth (bud) from a parent cell. As the bud is formed, the nucleus of the parent cell divides and one daughter nucleus migrates into the bud. The bud increases in size, while still attached to the parent cell and eventually breaks off and forms a new individual. It is common in yeasts. (*Saccharomyces* sp.).



Scanning electron micrograph of the budding yeast *Saccharomyces cerevisiae*.

4. Production of asexual spores

Reproduction by the production of spores is very common in many fungi.

SPORES

The term 'spore'(Gr. spora=seed, spore) is applied to any small propagative, reproductive or survival unit, which separates from a hypha or sporogenous cell and can grow independently into a new individual. Spores may be unicellular or multicellular. Multicellular spores are mostly with transverse septa and in some genera like *Alternaria* a spore will have both transverse and longitudinal septa. Each cell of a multicellular spore may be uninucleate, binucleate or multinucleate depending on the fungal species. The spores may be in different shapes and sizes.

They may be spherical, oval or ovate, obovate, pyriform, obpyriform, ellipsoid, cylindrical, oblong, allantoid, filiform or septicoid, falcate or fusiform. The spores may be with or without simple or branched appendages. The spores may be motile or nonmotile. If the spores are motile they are called planospores (Gr. Planets = wanderer) and non-motile spores are called aplanospores. Spores may be thin or thick-walled, hyaline or coloured, smooth or with ornamented walls. The following types of ornamentations are found on the walls.

Asexual spores

The spores produced asexually means are:

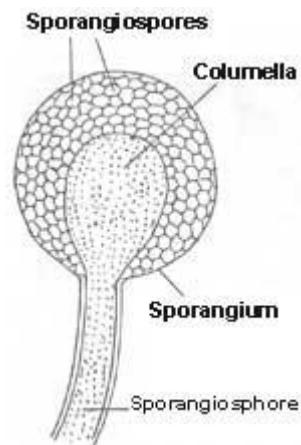
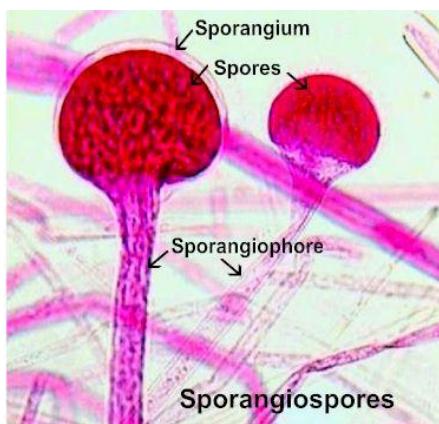
a. Sporangiospores

b. Conidia

c. Chlamydospores

a. Sporangiospores

Sporangiospores may be motile (planospores) or non-motile spores (aplanospores). In simpler fungi sporangiospores are usually motile and are called zoospores. These spores are produced in lower fungi, which inhabit aquatic or moist terrestrial substrates. Sporangiospores are formed in globose or sac-like structure called sporangium (pl. sporangia; Gr. Spora = seed, spore + angeion = vessel). In the zygomycetes and especially in the



Mucorales, the non-motile asexual spores called aplanospores are contained in globose sporangia surrounding a central core or columella. Sporangia are also known in which there is no columella, or where the spores (aplanospores) are arranged in a row inside a cylindrical sac termed a *Merosporangium* (e.g. *Syncephalastrum* spp. Mucorales).

These aplanospores may be uni or multinucleate and are unicellular, generally smooth-walled, globose or ellipsoid in shape. When aplanospores mature, they may be surrounded by mucilage and rain splash or insects usually disperse such spores. When aplanospores are dry then are dispersed by wind currents. The sporangiospores for sporangium may vary from several thousands to only one. In some fungi few-spores sporangia are called *Sporangiola*. *Sporangiola* are dispersed as a unit. e.g. *Choanephora* sp. and *Blakeslee* sp. in Choanephoraceae of Mucorales. In holocarpic thalli, the entire thallus (without differentiation of a sporophore) becomes a sporangium. Its contents cleave into a number of segments which round off and become zoospores. In eucarpic thalli, a part of the thallus, or special branches from thallus, function as or produce sporangia.

In terrestrial and plant parasitic forms of lower fungi, the sporangium may function as spore and no zoospores are formed. In others zoospores are formed within the sporangium itself or the inner wall of the sporangium may grow out into a short or long tube which swells to form a vesicle. The contents of the sporangium move into a vesicle and the zoospores are differentiated. E.g. *Pythium aphanidermatum*.

Zoospore (Gr. *Zoon* = animal + *spora* = seed, spore)

It is an asexually produced spore, which is motile by means of flagellum or flagella. Zoospore is naked and its covering is only a hyaloplasm membrane. Normally, zoospores are uninucleate and haploid. Zoospores may be spherical, oval, pyriform, obpyriform, elongate or reniform in shape. The zoospores are provided with one or two flagella (sing. flagellum, L. *flagellum*=whip) for its movement in the surrounding film of water. Flagellum is a hair-or tinsel-like structure that serves to propel a motile cell.

These flagella may be anterior, posterior or laterally attached to a groove in the body. There are two types of flagella in zoospores. They are whiplash and tinsel types. The whiplash flagellum has a long rigid base composed of all the eleven fibrils and a short flexible end formed of the two central fibrils only. The tinsel flagellum has a rachis, which is covered on all sides along its centre length with short fibrils. In uniflagellate zoospores the flagellum may be anterior

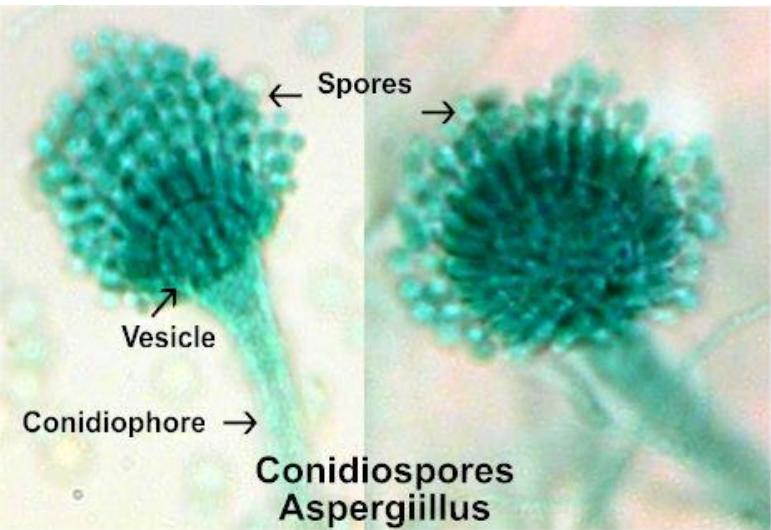
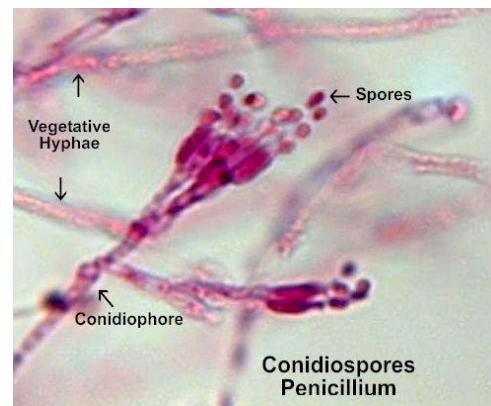
or posterior. But in biflagellate zoospores one is whiplash and the other is tinsel type and one points forward and the other backward. But in Plasmodiophorales fungi flagella are of whiplash type and unequal.

Zoospores pass through the three phases viz., motility, encasement and germination. The length of their motility depends on available moisture, temperature and presence of stimulatory or inhibitory substances in the environment. Later the zoospores become sluggish, spend or cast their flagella (except in chytridiaceous fungi and primary zoospores in Saprolegniales where flagella are shed but withdrawn into its body become spherical and secrete thin wall around itself and become encysted. The encysted zoospores germinate. The functions of zoospores include initiation of new generation and acting as gametes.

b. Conidiospores

Conidiospores or conidia (sing. Conidium) are asexual reproductive structures borne on special spore bearing hyphae conidiophores. They are found in many different groups of fungi, but especially in Ascomycotina, Basidiomycotina and Deuteromycotina. In Deuteromycotina conidia are the only means of reproduction. Conidia may be borne singly or in chains or in cluster. They vary from unicellular (e.g. *Colletotrichum*), bicellular, microconidia of *Fusarium* spp. and multicellular (*Pestalotiopsis*, *Cercospora*). One-celled spores are called amerospores, two celled spores are didymospores and multicellular spores are called phragmospores. The multicellular conidia may be divided by the septa in one to three planes. In *Alternaria* spp., conidia are with both transverse and longitudinal septa are called dictyospores.

The shape of the conidium may vary. They may be globose, elliptical, ovoid, cylindrical, branched or spirally coiled or star-shaped (staurospores). The colour of the conidia may be



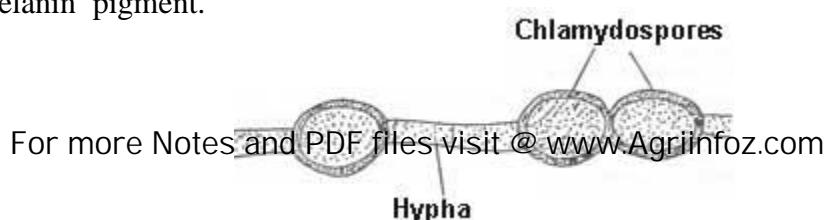
hyaline (hyalospore) or coloured (phaeospore) pink, green, or dark. The dark pigments are probably melanins. The colour of the conidia and conidiophores are important features used in classification. In the order Entomophthorales (e.g. *Basidiobolus*, *Pilobolus*) asexual reproduction is by means or forcibly discharged uninucleate or multinucleate primary conidia. On germination primary conidia develops uninucleate or binucleate secondary conidia. In species of *Fusarium* one or two-celled microconidia and many-celled macroconidia are common.

Conidia may be formed in acropetal (oldest conidium at the base and the youngest at the apex) or basipetal (oldest conidium at the apex and youngest at the base) succession. Generally the term 'conidia' is used for any asexual spores other than sporangia and spores formed directly by hyphal cells. When the spore is not much differentiated from the cells of the conidiophore in shape the term oidium is often used for conidia. A distinction between sporangiospores and conidia is that, before germination of sporangiospores a new wall, eventually continuous with the germ tube, is laid down within the original spore wall whilst in conidia there is no new wall layer laid down. Conidiophores are also known as sporophores. They are special hyphae bearing conidia.

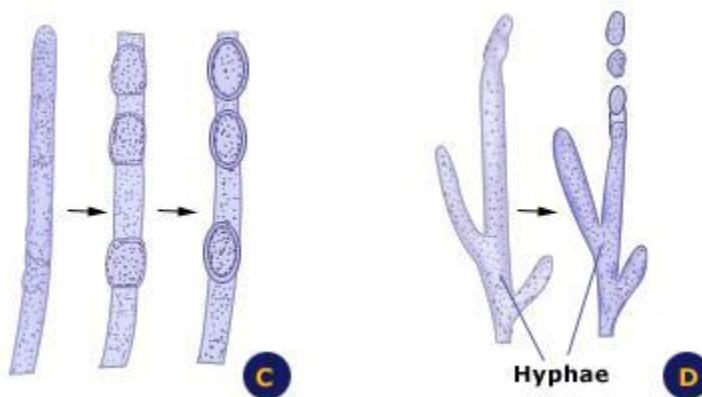
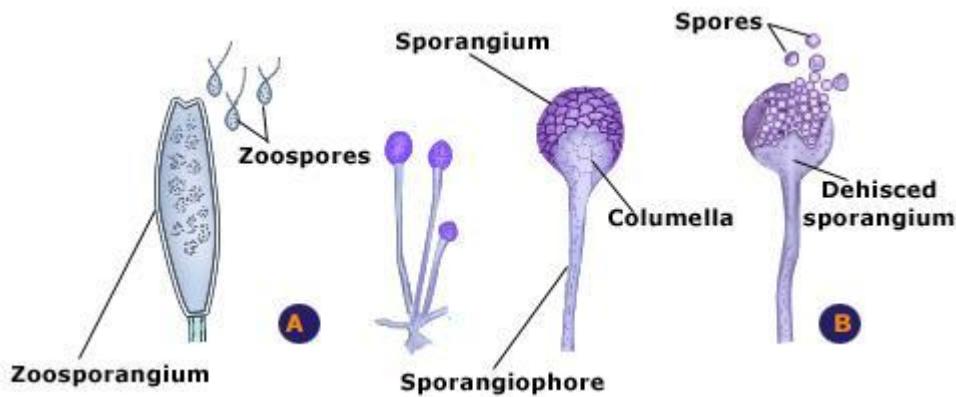
They may be free, simple or branched. They may be distinct from each other or may be aggregated to form compound sporophores or fruiting bodies such as synnemata, sporodochia, acervuli and pycnidia. They may be provided with sterigmata or specialized branches on which they bear conidia. Some conidial spores are inflated at the tips (e.g. *Aspergillus*); others are inflated at intervals, forming kneelike structures on which the conidia are grouped (*Gonatobotrys*); still others have many branches, which are characteristically arranged, in whorls (*Verticillium*) or in sympodium (*Monopodium*). They are generally produced on the surface of the host. The sporogenous part of the conidiophore is commonly apical but may be laterally placed. The apical zone of differentiation of conidiophore may give rise to a single conidium or more often, to a succession of conidia in chains, false heads.

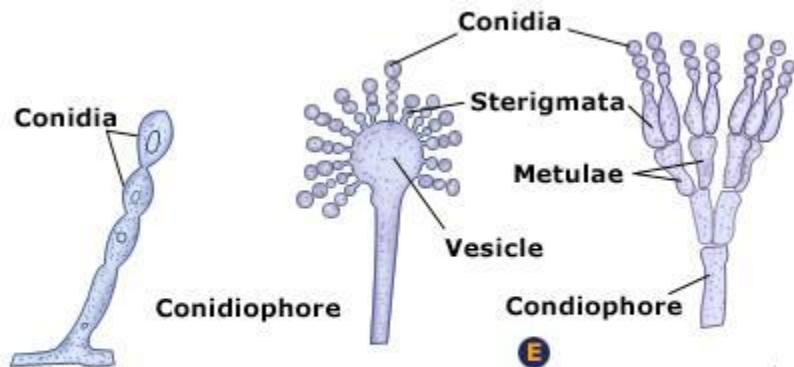
c. Chlamydospores

Chlamydospore (Gr. *Chlamys* = mantle + *spora* = seed, spore) is a thick-walled thallic conidium that generally function as a resting spore. Terminal or intercalary segments or mycelium may become packed with food reserves and develop thick walls. The walls may be colourless or pigmented with dark melanin pigment.



These structures are known as chlamydospores. e.g. *Fusarium*, *Mucor racemosus*, *Saprolegnia*. Generally there is no mechanism for detachment and dispersal of chlamydospores. They become separated from each other by the disintegration of intervening hyphae. They are the important organs or asexual survival in soil fungi. When chlamydospores are found in between fungal cells they are called 'intercalary chlamydospores'. Chlamydospores produced at the apex of the hypha are called 'apical or terminal chlamydospores'.





**A. Zoospores; B. Sporangiospores; C. Chalmydospores;
D. Oidia; E. Conidia**

SEXUAL REPRODUCTION

Sexual reproduction in fungi involves union of two compatible nuclei. The nuclei may be carried in motile or non-motile gametes, in gametangia or in somatic cells of the thallus.

Phases of sexual reproduction

Three typical phases occur in sequence during the sexual reproduction.

1. Plasmogamy

In plasmogamy (Gr. *plasma*=a molded object, i.e. a being + *gamos* = marriage, union) anastomosis of two cells or gametes and fusion of their protoplasts take place. In the process the two haploid nuclei of opposite sexes (compatible nuclei) are brought together but the nuclei will not fuse.

2. Karyogamy

The fusion of two haploid nuclei brought together as a result of plasmogamy is called karyogamy (Gr. *karyon* = nut, nucleus + *gamos* = marriage). This stage follows immediately after plasmogamy in many of the lower fungi or may be delayed in higher fungi. In higher fungi plasmogamy results in a binucleate cell containing one nucleus from each cell. Such a pair of nuclei is called dikaryon (NL. *Di* = two + Gr. *karyon* = nut). These two nuclei may not fuse until later in the life history of the fungus. Meanwhile, during growth and cell division of the binucleate cell, the dikaryotic condition may be perpetuated from cell to cell by conjugate division of the two closely associated nuclei and by the separation of the resulting sister nuclei with two daughter cells. Nuclear fusion, which eventually takes place in all sexually reproducing fungi, is followed by meiosis.

3. Meiosis

Karyogamy results in the formation of a diploid ($2n$) nucleus. Meiosis (Gr. *meiosis*=reduction) reduces the number of chromosomes to haploid and constitutes the third phase of the sexual reproduction. This nucleus undergoes a reduction division to form two haploid nuclei each with ' n ' chromosomes. A mitotic division follows and four nuclei are formed. In ascomycetes another nuclear division takes place resulting in the formation eight nuclei. The nuclei get surrounded by a small amount of cytoplasm and secrete a wall to become spores.

In a true sexual cycle, the above three phases occur in a regular sequence and usually at specified points. If there is only one free living thallus, haploid or diploid in the life cycle of a fungus is called haplobiontic (Gr. *haplos* = single + *bios* = life). e.g. Oomycetes haploid gamete and diploid mycelium. If a haploid thallus alternates with a diploid, the life cycle is called diplobiontic (Gr. *diplos* = double + *bios* = life). e.g. *Allomyces* (water mold *Coelomomyces*, mosquito parasite) and in some yeasts.

Organs involved in sexual reproduction

Fungi, which produce morphologically distinguishable male and female sex organs in each thallus, are called hermaphroditic (Gr. *hermes* = the messenger of the Gods, symbol of the male sex + *aphrodite* = the Goddess of love, symbol of female sex) or monoecious or *unisexual* (Gr. *monos* = single, one + *oikos* = dwelling, home). A single thallus of a monoecious fungi can reproduce sexually by itself if it is self-compatible. In a fungus when the female and male organs are produced on two different thalli it is said to be dioecious or bisexual. (Gr. *dis* = twice, two + *oikos* = home; i.e.; the sexes separated into two different individuals). Normally a single thallus of a dioecious fungus cannot reproduce sexually by itself as the thallus is either male or female.

The sex organs of fungi are called gametangia (sing. gametangium; Gr. *gambetes* = husband + *angeion* = vessel, container). Sex cells are called gametes and the mother cells (sex organs) are called gametangia. If the gametes and gametangia produced are morphologically identical or similar they are called as isogametes (Gr. *ison* = equal) and isogametangia respectively. When the gametes and gametangia produced differ in size and structure (morphologically different) they are called heterogametes (Gr. *heteros* = other, different) and heterogametangia respectively. In the latter case, the male gametangium is called antheridium (pl. antheridia; Gr. *antheros* = flowery + *idion*, dimin. suffix) and the female gametangium is

called oogonium (pl. oogonia; Gr. *oon* = egg + *gonos* = offspring). The male gamete is known as antherozoid or sperm and the female as an egg or oosphere.

Methods of sexual reproduction

The following are the five methods, which the fungi employ to bring the compatible nuclei together for fusion.

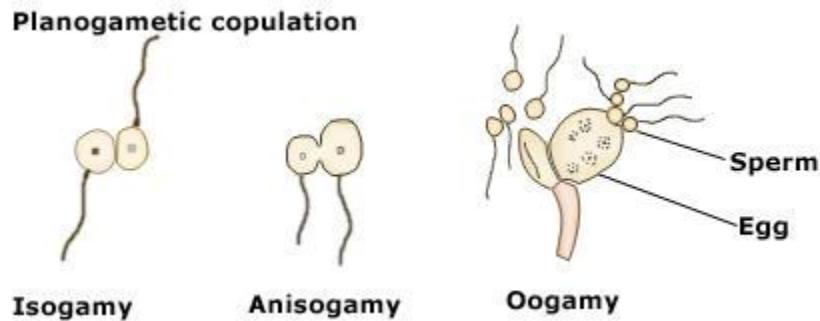
1. Planogametic copulation
2. Gametangial contact (Gametangy)
3. Gametangial copulation (Gametangiogamy)
4. Spermatization
5. Somatogamy

1. Planogametic copulation or conjugation

A planogamete is a motile gamete or sex cell. The fusion of two gametes, one or both of which are motile is called planogametic copulation. This type of sexual reproduction is common in aquatic fungi. There are three different types of planogametic copulation.

a. Copulation of isogamous motile gametes

In this type morphologically similar but compatible type of mating type of gametes unite to form a motile zygote. e.g. *Synchytrium*.



b. Copulation in anisogamous motile gametes

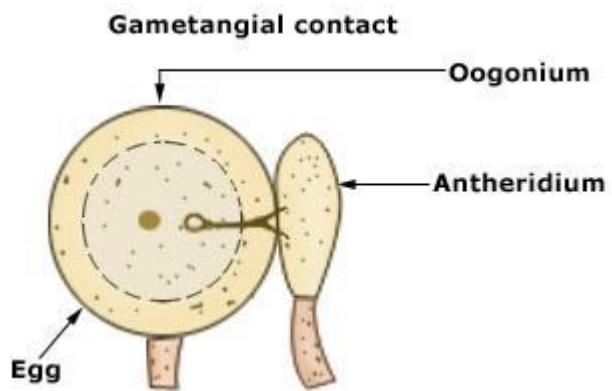
It involves union of one larger gamete with another smaller gamete. The resultant zygote is motile. The zygote resulting from isogamous or anisogamous planogametic copulation forms a 'resting sporangium'. On further development it functions as sporangium by differentiating zoospores internally.

c. Heterogamous planogametic copulation

In this type, a non-motile female gamete (oosphere) is fertilized by a motile male gamete. This results in the formation of oospores, a resistant structure and resting spore. Oospores germinate and produce mycelium directly.

2. Gametangial contact

In this method the male gamete (antheridium) and the female gamete (oogonium) come in contact and one or more nuclei from the male gamete enter the female gamete, oogonium dissolved in the intervening wall through

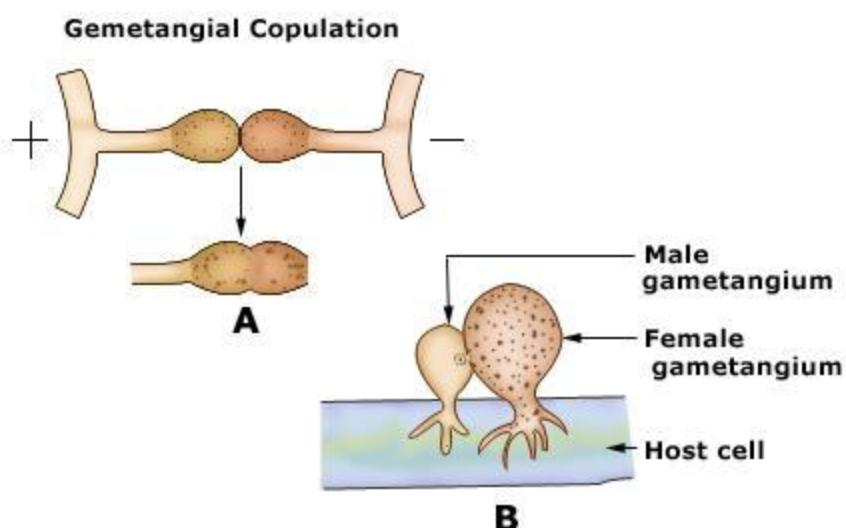


a pore or through a fertilization tube. In no case the gametangia actually fuse or lose their identity during the sexual act. e.g. Fungi in Peronosporales. Gametangial contact is also common in some Ascomycotina where antheridia and female organs (archigonia or ascogonia) may or may not be well defined.

3. Gametangial copulation: This is a process of fusion of entire contents of the two mating gametangia. There are two types.

a. Mixing of entire protoplasm of male and female gametangia

Two gametangia meet and their entire contents fuse in the female gametangium leading to formation of a zygote. The zygote forms a resting sporangium. e.g. Aquatic fungi (Chytridiomycetes).



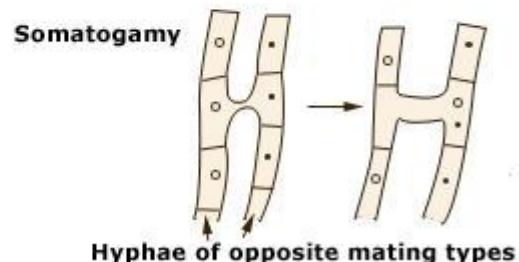
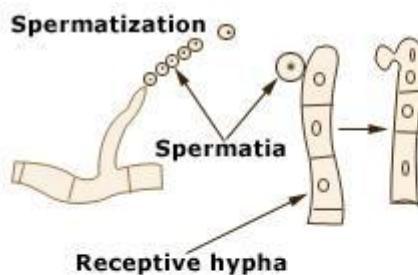
b. Isogamous copulation

Two morphologically similar gametangial hyphae come in contact, the wall at the point of contact dissolves and the contents mix in the cell thus formed. This results in the formation of zygosporangium. e.g. *Mucor*, *Rhizopus*, *Phycomyces*.

4. Spermatization

Some fungi like rusts bear numerous minute, non-motile uninucleate, male cells called spermatia. (sing. spermatium; Gr. *spermation*=little seed)

Spermatia are produced in spiral receptacles called spermagonia (sing. spermagonium; Gr. Sperma =seed, sperm+ gennao=I give birth) or pycnia (sing.



pycnium; Gr. *pycnos*=concentrated). Insects, wind or water to the female gametangium carries them, which is usually a special receptive hypha (or trichogyne) to which they become attached. A pore develops at the point of contact and the contents of spermatium pass into the particular respective hyphae. This results in plasmogamy and initiation of the dikaryotic stage of the cell.

5. Somatogamy

In somatogamy two sex organs are produced and somatic cells function as gametes somatogamy (Gr. *soma* = body + *gamos* = marriage, union) hyphae anastomose and the nuclei of opposite mating type are brought together in one cell. Somatogamy is common in Ascomycotina and Basidiomycotina fungi.

Heterokaryosis

The phenomenon of existence of different kinds of nuclei in the same individual is known as heterokaryosis. (Gr. *heteros* = other+ *karyon*=nut, nucleus). The individual which exhibit heterokaryosis is called heterokaryon or heterokaryotic. It has been demonstrated in numerous Ascomycetes, Basidiomycetes and Fungi Imperfecti (Davis, 1966). In a heterokaryotic individual, each nucleus is independent of all other nuclei, but the structure and behaviour of the

individual appear to be controlled by the kinds of genes it contains and the proportion of each kind. Heterokaryosis may arise in a fungal thallus in four ways:

1. By the germination of a heterokaryotic spore, which will give rise to a heterokaryotic soma.
2. By the introduction of genetically different nuclei into homokaryon (Gr. homo=same + karyon = nut, nucleus), a soma in which all nuclei are similar.
3. By mutation, in a multinucleate homokaryon. The mutant nuclei subsequently survive, multiply and spread among the wild-type nuclei.
4. By fusion of some nuclei in a haploid homokaryon to form diploid nuclei which subsequently survive, multiply and spread among the haploid nuclei. Thus in some fungi it is possible to have different kinds of haploid nuclei in the same soma and a mixture of haploid and diploid nuclei. In most fungal individuals, the haploid and diploid phases of the life cycle are clearly distinguishable.

Parasexuality or parsexual cycle

Some fungi (Deuteromycetes) do not go through a sexual cycle but derive many of the benefits of sexuality through parasexuality (Gr. *para* =beside+sex). This is a process in which plasmogamy, karyogamy and haploidization takes place, but not at specified points in the thallus or the life cycle of an organism. Parsexual cycle is very important in Deuteromycetes where sexual reproduction does not take place. Some fungi, which reproduce sexually, also exhibit parasexuality.

Pontecorvo and Roper from the University of Glasgow in *Aspergillus nidulans*, the imperfect stage of *Emericella nidulans* first discovered parsexual cycle in 1952. Since then it has been reported in number of fungi in Ascomycotina, *Cochliobolus sativus*, (imperfect state: *Bipolaris sorokiniana* (syn . *Helminthosporium sativum*) *Leptosphaeria maculans* etc.), *Basidiomycotina* *Puccinia graminis*, *Melampsora lini*, *Ustilago maydis*, *U. hordei*, *Schizophyllum commune*, *Coprinus lagopus* and Deuteromycotina. *Ascochyta imperfecta*, *Aspergillus amstelodami*, *A. fumigatus* , *A. rugulosus*, *A. oryzae*, *A. sojae*, *A. niger* , *Fusarium oxysporum* f.sp. *cubense*, *F. oxysporum* f.sp. *callistephi*, *Phymatotrichum omnivorum*, *Pyricularia oryzae*, *Penicillium italicum*, *Penicillium chrysogenum* *Verticillium albo-atrum*.

The sequence of events in a complete parsexual cycle is as follows.

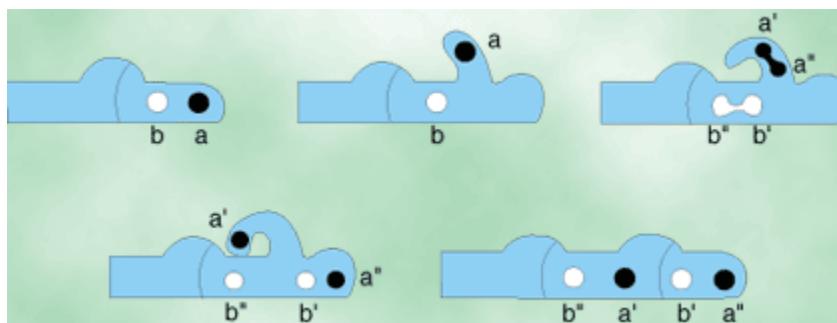
1. Formation of heterokaryotic mycelium
2. Fusion between two nuclei
 - a. Fusion between like nuclei
 - b. Fusion between unlike nuclei
3. Multiplication of diploid nuclei side by side with the haploid nuclei
4. Occasional mitotic crossing-over during the multiplication of the diploid nuclei
5. Sorting out of diploid nuclei
6. Occasional haploidization of the diploid nuclei
7. Sorting out of new haploid strains

Anastomosis

The important cause for heterokaryosis is anastomosis. Anastomosis involves fusion of hyphae of some species, movement of one or more nuclei into one or the other of the fused cells, and the establishment of a compatible heterokaryotic state. A similar nuclear displacement may occur in adjacent cells of the same hypha by formation of clamp connections through which nucleus or nuclei from one cell move into another.

Clamp connection

Clamp connection is a mechanism found in Basidiomycetes. It is a bridge-like hyphal connection characteristic of the secondary mycelium in many Basidiomycetes. It ensures that sister nuclei arising from conjugate division of the dikaryon become separated into two daughter cells. Clamp connections are found during nuclear division and supposed to help in dikaryotization of adjacent cells.



Sexual spores

The sexual spores are formed as a result of fusion between two opposite sex gametes. They are resting spores, incapable of germination immediately after formation. Sexual spores are

oospores, zygosores, ascospores and basidiospores desiring their names from the class to which the fungi belong.

1. Oospores

An oospore (Gr. *oon* = egg + *spora* = seed, spore) is a sexually produced spore, which develops from unequal gametangial copulation or markedly unequal gametic fusion. It is the characteristic sexually produced spore of oomycetes. Oospores develop from fertilized oospheres (Gr. *oon* = egg + *sphaira* = sphere). One or more oospheres develop within 'oogonia', which are multinucleate, globose and female gametangia



2. Zygospores

Zygospores (Gr. *zygos* = yoke + *spora* = seed, spore) are sexually produced resting spores or structures formed as a result of plasmogamy between two gametangia, which are usually equal in size. They are resting structures. Zygospores are the typical sexually produced spores of Zygomycetes e.g. Mucorales and Entomophthorales. Zygospores are often large, thick-walled, warty structures with large food reserves and are unsuitable for long distance dispersal.



3. Ascospores

Ascospores (Gr. *askos* = sac + *spora* = seed, spore) are the characteristic spores of the large group of fungi known as Ascomycotina. They are formed as a result of nuclear fusion immediately followed by meiosis. The four haploid daughter nuclei then divide mitotically to give eight haploid nuclei around which the ascospores are cut out. In most ascomycetes, the eight ascospores are contained within a cylindrical sac or ascus from which they are forcible ejected by a squirting process in which the ascus contents, consisting of ascospores and ascus sap, are ejected by explosive breakdown of the tip of the turgid ascus whose elastic walls contract.

Ascospores vary greatly in size, shape, colour and wall ornamentation. In size, the range is from $4-5 \times 1\mu\text{m}$ in small-spored forms such as minute cup fungus, *Dasyscyphus* to $130 \times 45\mu\text{m}$ in lichen, *Pertusaria pertusa*, which is a symbiotic association between an ascomycete and a green alga. Ascospore shape varies from globose, oval, elliptical, lemon shaped sausage-

shaped, cylindrical or needle-shaped. Ascospores may be uninucleate or multinucleate, unicellular or multicellular, divided up by transverse or by transverse and longitudinal septa.

The wall may be thin or thick, hyaline or coloured, smooth or rough, sometimes folded into reticulate folds and may have a mucilaginous outer layer which may be extended to form simple or branched appendages. In general, ascospores are resting structures, which survive adverse conditions. They may have extensive food reserves in the form of lipid and sugars such as trehalose.

Ascus

Ascus (pl. *asci*; Gr. *askos* = sac) is a sac-like cell generally containing a definite number of ascospores (typically eight) formed by free cell formation usually after karyogamy and meiosis. In the large majority of the Ascomycetes the asci are elongated, either club-shaped or cylindrical. But globose, ovoid or rectangular asci are also found. Ordinarily the ascus represents a single cell in which the ascospores are formed. Asci may be stalked or sessile, they may arise from a common fascicle and spread out like a fan or they may arise simply at various levels within the fruiting body.



Development of ascus

Ascus develops from a specialized hypha called, ascogenous hypha, which in turn develops from an ascogonium. The ascogenous hypha is multinucleate, and its tip is recurved to form a crozier (Shepherd's crook). Within the ascogenous hypha nuclear division occurs simultaneously. Two septa at the tip of the crozier cut off a penultimate cell destined to become an ascus. The terminal cell of the crozier curves round and fuses with the ascogenous hypha behind the penultimate cell, and this region of the ascogenous hypha may grow on to form a new crozier in which the same sequence of events is repeated. Repeated proliferation of the tip of the crozier can result in a cluster of asci. In the ascus initial the two nuclei fuse and the fusion nucleus undergoes meiosis to form four haploid daughter nuclei.

These nuclei then undergo a mitotic division so that eight haploid nuclei result. During these nuclear divisions the ascus is elongating and the plane of the division is parallel to the length of the ascus. Cytoplasm is cleared out around each nuclei to form an ascospore. In some

forms the eight nuclei divide further so that each ascospore is binucleate. Where the ascospores are multicellular there are repeated nuclear divisions. In some forms more than eight ascospores are formed or the eight ascospores may break up into part-spores. Double membranes form a cylindrical envelope lining the young ascus. The lining layer is termed as ascus vesicle or ascospore membrane. Between the two layers forming the membrane, the spore wall is secreted, and the inner membrane forms the plasma membrane of the ascospore.

The forms of asci vary. The ascus with non-explosive ascospore release is often a globose sac. But in the majority of the Ascomycetes, the ascus is cylindrical and the ascospores are expelled from the ascus explosively. It is thought that the explosive release follows increased turgour caused by water uptake. In many cases the asci are surrounded by packing tissue in the form of paraphyses, pseudoparaphyses and other asci, so that they can expand laterally but are forced to elongate. In the cup fungi or Discomycetes the elongation of asci raises their tips above the general level of the hymenium. The ascus tips are often phototropic and when the increased pressure causes the ascus tip to burst, the spores are shot out in a drop of liquid, the ascus sap. In this group, a large number of asci may be charged simultaneously, so that a cloud of ascospores is visible. This phenomenon is known as puffing. In some Discomycetes (e.g. the Pezizales) the ascus tip is surrounded by a cap or operculum, which is blown aside or actually blown off the tip of the ascus by the force of explosion. However, in other Discomycetes (e.g. the Helotiales) the ascus tip is perforated by a pore and there is no operculum. These two types of asci are respectively termed *operculate* and *inoperculate* and the presence or absence of an operculum is an important feature of classification.

In a flask-fungi (Pyrenomycetes) the asci are enclosed in a cavity, which opens to the exterior through a narrow pore, the ostiole. As an ascus ripens, it elongates and takes up a position inside the ostiole, often gripped in position by a lining layer of hairs, periphyses. In this case the asci discharge their spores singly and puffing does not happen.

Asci of Pyrenomycetes are never operculate in many groups, the ascus tip has a distinctive apical apparatus. In many pyrenomycetes, there is an apical ring or annulus when the ascus explodes, the apical ring is everted and is believed to grip the ascospores as they are ejected. If the wall of the ascus is single it is called unitunicate and if the wall of the ascus is double it is called bitunicate. Loculoascomycetes have bitunicate asci. In bitunicate asci there are two wall layers, which physically separate from each other. The outer layer is termed or

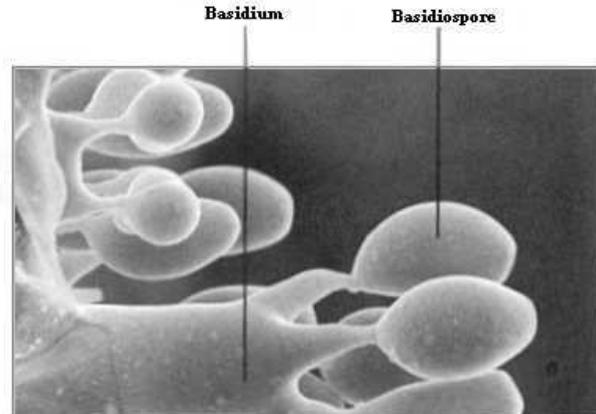
ectoascus or ectotunica and the inner layer is called the endoascus or endotunica. Both the layers are made up of microfibrils embedded in an amorphous matrix. The two layers differ only in the arrangement of microfibrils.



Ascospores of *Venturia inaequalis* in ascospores.

4. Basidiospores

Basidiospore (Gr. *Basidion* = small base + *spora* = seed, spore) is a spore borne on the outside of a basidium, following karyogamy and meiosis. Basidiospores are more uniform compared to ascospores. Typically they are unicellular, but transversely septate spores are found in certain groups like Dacrymycetaceae (Reid, 1974). In shape, they vary from globose, sausage-shaped, fusoid, almond-shaped (i.e. flattened) and the wall may be smooth or ornamented with spores, ridges or folds. The colour of basidiospores is an important criterion of classification.



They may be colourless, white, cream, yellowish, brown, pink, purple or black. The spore colour may be due to coloured substances in the cytoplasm of the spore or in the spore wall. This explains the change of colour of a mushroom gill from pink when immature, due to cytoplasmic spore pigments to purple when mature due to wall pigments.

The spore is attached to the basidium at the tip of a ‘sterigmata’, a curve horn -like prong projecting from the apex of the basidium. The spore is projected for a short distance from a basidium. The point at which the spore is attached to the sterigma is ‘hilum’. Hilum is usually found at the tip of a short conical projection, the ‘hilar appendix’ (Fig.31). The term ballistospores is used to describe basidiospores, which are violently projected from their sterigmata. Most basidiospores are ballistospores and in Gasteromycetes basidiospores are not projected violently.

Basidium (pl. basidia, Gr. *basidion* = a small base) is a spore bearing structure bearing on its surface a definite number of basidiospores (typically four) that are usually formed following karyogamy and meiosis. In contrast with the endogenous spores of the ascus, basidia bear spores exogenously, usually on projections called ‘sterigmata’. The number of spores per basidium is typically four, but two spored basidia are quite common. There may be nine spores per basidium in *Phallus impudicus*.

Basidia vary in structure and the form of the basidium is an important criterion in classification. In the toadstools the basidium is a single cylindrical cell, undivided by septa, typically bearing four basidiospores at its apex. Such basidia are called ‘holobasidia’

In the Uredinales and Ustilaginales the basidium develops from a thick-walled cell (teliospore or chlamydospore) and is usually divided into four cells by three transverse septa. Transversely segmented basidia are also found in the Auriculariaceae, but here the basidia do not arise from resting cells. In the Tremellaceae, the basidia are longitudinally divided into four cells, while in the Dacrymycetaceae the basidium is unsegmented but forked into two long arms, to form the tuning type of basidium. Segmented basidia are sometimes termed phragmobasidia (or heterobasidia).

Development of basidium

The development of basidium is well illustrated in *Oudemansiella radicata* (Syn. *Collybia radicata*) (Fig.30). The basidium arises as a terminal cell of a hypha making up the gill tissue on the underside of the cap of the fruit body. The basidia are packed together to form a fertile layer or hymenium. A basidium is at first densely packed with cytoplasm, but soon several small vacuoles appear. Later, a single large vacuole develops at the base of the basidium and, by the enlargement of this vacuole, cytoplasm is pushed towards the end of the basidium. A clear

cap is visible at the tip and it is here that the sterigmata develop. In the fully developed basidium the spores are full of cytoplasm while the body of the basidium contains only a thin lining of cytoplasm, surrounding an enlarged vacuole. Young basidia are binucleate, and nuclear fusion occurs here. The resulting fusion nucleus undergoes meiosis immediately, so that four haploid daughter nuclei result, and one is distributed to each basidiospore. In some basidia a mitotic division follows meiosis, so that some basidiospores are binucleate.

Reproductive structures

Fungi reproduce by means of their propagules. In most fungi the propagules are differentiated as spores. But in some fungi the stromatic aggregations of hyphae like the sclerotia also perform the function of propagation. The simple or branched spore-bearing hyphae are known as sporophores, but in some fungi the spores may be formed directly by the hyphal cell e.g. chlamydospores. In general spore formation starts when the vegetative growth has reached a certain development.

Types of sporophores

Spore bearing or sporogenous organs (sporophores) develop as special branches from the vegetative hyphae. There are two types of sporophores viz., simple and compound. The spore bearing branches usually arise vertically and may be distinctly branched. When these branches bear sporangia they are called sporangiophores (as in Oomycetes of Mastigomycotina and Zygomycotina). When the spore bearing branches bear conidia they are called conidiophores (as in Ascomycotina and Deuteromycotina). These sporangiophores and conidiophores are called simple or filamentous sporophores. Aggregation of hyphae from stromatic or semistromatic structures and grows into compound sporophores. They contain or bear layers of sporogenous cells and spores and form the fructifications and fruit bodies. e.g. stipes formed by germination of sclerotia in Ascomycotina and by higher basidiomycotina.

Fructifications and fruit bodies

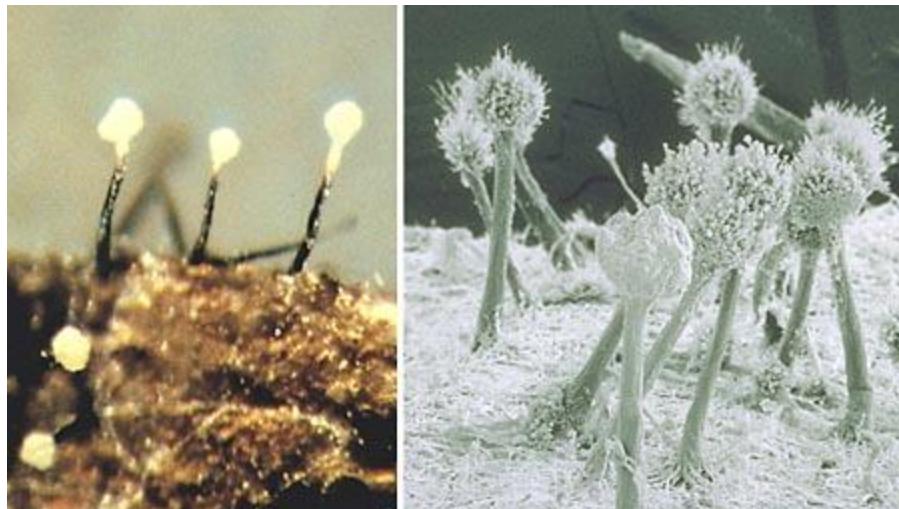
The sporophores bear fruiting bodies or form fructifications, which may be asexual or sexual in nature. In lower fungi (Plasmodiophoromycetes, Chytridiomycetes, Oomycetes and Zygomycotina) asexual spores are usually enclosed in simple sacs called sporangia or zoosporangia. In higher fungi (Ascomycetes and Basidiomycetes) complex aggregates of spore bearing hyphae are formed and supporting and protective tissues surround it. These complex structures are called as spore fruits or fructifications (*L. fructus* = fruit).

Asexual fructifications

In fungi conidiophores are grouped together to form specialized structures such as synnemata (sing. synnema) and sporodochia (sing. sporodochium) or produced in fructifications known as pycnidia (sing. pycnidium) and acervuli (sing. acervulus).

a. Synnema or coremium

Synnema or Coremium (pl. coremia) Consists of a group of conidiophores often united at the base and part way up the top. Conidia may be formed along the length of the synnema or only at its apex. The conidiophores comprising a synnema are often branched at the top with the conidia arising from the conidiogenous cells at the tips of the numerous branches. e.g. Deuteromycotina (*Arthrobotryum* sp (Fig), *Penicillium claviforme*, *Doratomyces stemonitis*, *Ceratocystis ulmi*.



synnema: (pl. synnemata; syn. coremium) compact or fused, generally upright conidiophores, with branches and spores forming a headlike cluster

[synnemata of *Ophiostoma (Graphium) ulmi*]

b. Sporodochium

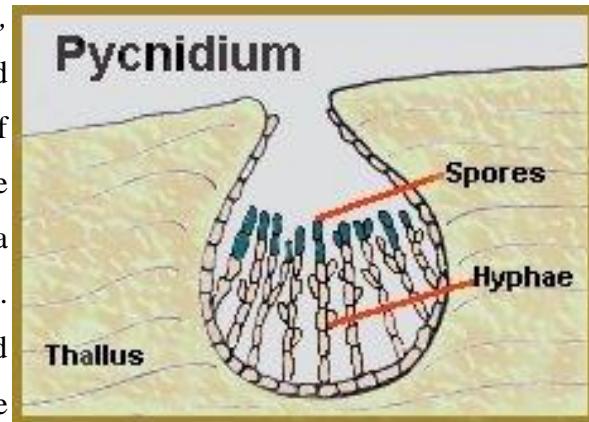
Sporodochium is a fruiting body in which conidiophores arise from a central cushion-like aggregation of hyphae. The conidiophores are packed tightly together and are generally shorter than those composing a synnema. e.g. *Epicoccum*, *Nectria*.

sporodochium: (pl. sporodochia)

Superficial, cushion-shaped asexual fruiting body consisting of a cluster of conidiophores

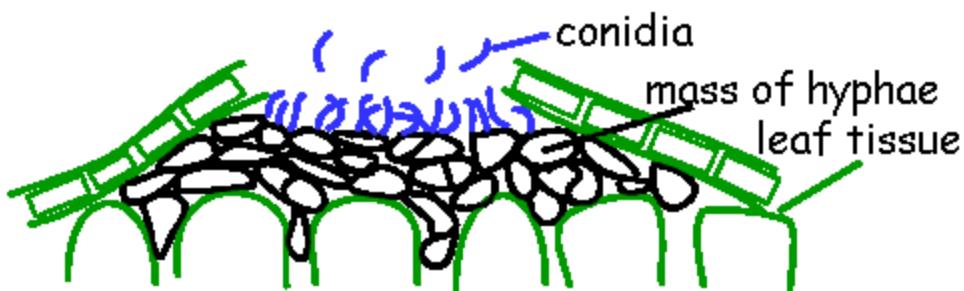
c. Pycnidium

Pycnidium is a globose or flask-shaped body, which is lined on the inside with conidiophores. e.g. *Septoria*, *Phoma*, *Ascochyta*, *Leptosphaeria*. Pycnidia may be completely closed or may have an opening. The opening or mouth of pycnidium is called ostiole (L. *ostiolum* = little door). They may be provided with a small papilla or with a long neck leading to the opening. Pycnidia vary greatly in size, shape, colour and consistency of the pseudoparenchymous wall. The wall of pycnidium is called peridium (pl. *peridia*; G. *peridion*=small leather pouch) and it is composed of multicellular layer, as fungal tissues. Pycnidia may be formed superficially or sunken in the substratum. They may be formed directly by the loose mycelium or may be definitely stromatic.



d. Acervulus

Acervulus (pl. *acervuli*) is a fruiting structure commonly found in the order Melanconiales (Deuteromycotina). It is typically a flat or saucer-shaped mass of aggregated hyphae bearing short conidiophores in a compact layer. Intermingled with the conidiophores, setae (sing. *seta*; L. *seta* = bristle) are found. Setae are long, pointed, dark coloured, sterile structures. In nature acervuli are produced on plant tissues subepidermally or subcuticularly and becomes erumpent on maturity. e.g. *Colletotrichum*.



Sorus

Sorus (pl. *sori*; Gr. *Soros* = heap) is a little heap of sporangia or spores. It may be naked or covered by a thin false membrane, as in smuts, or protected by the epidermis as in rust diseases or white blister or white rust (*Albugo* spp.). The structures break open at maturity and release the spores within, in the form of rust, which is characteristic of these diseases.

Sexual fruiting bodies

a. Pycnium

Pycnium or spermagonium (pl. pycnia; Gr. *pycnos* = concentrated) is a fruit body, which is similar to pycnidium and is formed in sexual cycle of rust fungi. Pycnia are produced from primary uninucleate mycelium growing in the tissues of the host. They may be determinate or indeterminate in growth and may form in a subcuticular, subepidermal or subcortical fashion. Pycnia may be flask-shaped, conical, flat and sprawling. The flask-shaped type is more typical. The mouth of the flask (called ostiole) is lined by a bunch of unbranched, tapering, pointed, orange coloured hairs called 'periphyses' (sing. *periphysis*; Gr. *peri* = around + *physis* = a being, a growth). Periphyses develop from the upper edge of spermagonal wall, converge toward a central point and curved upward.

The tips of the periphyses, pushing against the host epidermis from below, rupture it and protrude above it through the opening they have created. Among the periphyses thinner-walled and branched hyphae called flexuous hyphae or receptive hyphae are found. The pycnial wall cells send many closely -packed, elongated, tapering, unbranched uninucleate sporogenous cells or spermatiophores (Gr. *spermation* = little seed+ *phoreus*=bearer) in the cavity. These spermatiophores give rise to a series of uninucleate spermatia (sing. *spermatium* Gr. *spermation*=little seed) or pycnospores in a basipetal fashion.

Pycnospore is a non-motile, uninucleate, unicellular spore-like male structure that empties its contents into a receptive female structure during plasmogamy. Pycnospores are variously regarded as gametes or gametangia. The pycnospores produced in large numbers are exuded up, out of the pycnial cavity through the ostiole in a droplet of nectar (a thick, sticky, fragrant, sweet liquid). e.g. pycnium is produced by *Puccinia graminis tritici* in the alternate host, barberry (*Berberis vulgaris*).

b. Aecium

Aecium (pl. Aecia: Gr. *aikia* = injury) is also formed during sexual cycle. Aecium is a shallow or deep cup-shaped structure produced in a leaf and located in the lower portion and break through the lower epidermis. Aecia may be with or without peridium (Fig.38). It is a group of typically dikaryotic hyphal cells within the parasitized host that give rise to chains of dikaryotic aeciospores. Larger aeciospores are alternated with small, sterile intercalary cells or disjunctors.

In most rust fungi the peripheral cells of the aecial base successively divide and gives rise to a wall that surrounds the spore chain in the form of a cup. The wall is known as 'peridium'. In a young aecium that has not broken the host epidermis, the peridium surrounds the spore chain on all sides, forming a complete dome over them. When the aecium matures, the spore chains push through the roof of the peridium and the aeciospore are released. The torn peridium forms a lip-like structure around the aecial cup.

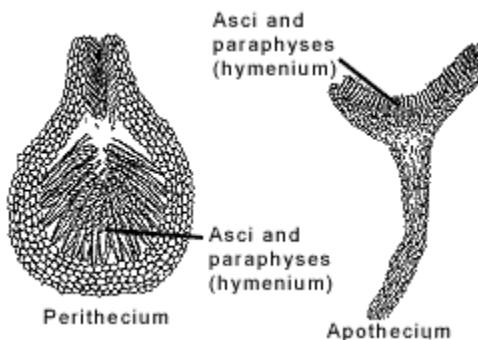
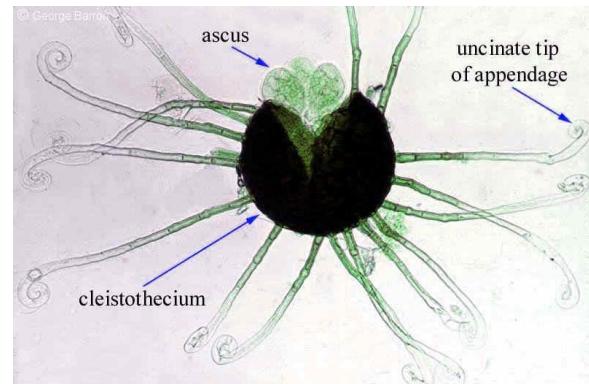
c. Ascocarps

Ascocarp (Gr. *askos* = sac+ *karpos* =fruit) is a fruiting body that contains asci and ascospores. Ascomycetes fungi with few exceptions produce ascocarps. They are in various forms like spherical, flask-shaped, cup-and saucer shaped and pod-shaped. They may be closed in some, and provided with a narrow wide opening in others. Ascocarps may be formed singly or in groups. They may be superficial, erumpent or deeply embedded in the substratum. The substratum may be composed entirely of host tissue, or it may be a hyphal stroma or in which the ascocarps form. There are four categories ascocarps.

i. **Cleistothecium:** Asci are produced in completely closed ascocarp.

ii. **Perithecium:** It is more or less closed ascocarp; but at maturity it is provided with ostiole through which the ascospores escape.

iii. **Apothecium:** Ascocarp produce asci in open.



iv. **Ascostroma or Pseudothecium:** Stromatic ascocarp, which bears asci directly in locules within the stroma.

i. **Cleistothecium:** (pl. cleistothecia; Gr. *kleistos* = closed + *theke* = case).

Cleistothecium or cleistocarp is a closed ascocarp and has no ostiole. It is deep brown to black in colour, more or less spherical and often provided with appendages on its body, which serve as organs of anchorage and help in dissemination. They may contain one to several asci, which discharge their spores violently. Each cleistothecium of *Sphaerotheca* and *Podosphaera* contains a single ascus whereas each cleistothecium in *Erysiphe*, *Microsphaera*, *Uncinula*, *Leveillula* and *Phyllactinia* contain several asci. Cleistothecia crack open at maturity by swelling of the contents. They are found in Eurotiales and Erysiphales (powdery mildews or white mildews or true mildews). The matured cleistothecia of most Erysiphaceae are provided with characteristic appendages that vary considerably in length and character, and which together with the number of asci developed in the cleistothecium, form the basis for differentiation of genera. Cleistothecial appendages are of four types viz.

Myceloid appendages: Appendages resemble somatic hyphae in flaccidity and indefinite growth. e.g. *Erysiphe*, *Sphaerotheca* and *Leveillula*.

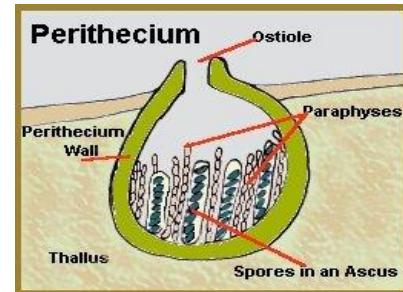
Appendages are rigid, spear-like with a bulbous base and pointed tip. e.g. *Phyllactinia*.

Appendages are rigid with curved tips e.g. *Uncinula*, *Pleochaeta*.

Appendages are rigid with dichotomously branched tips. e.g. *Microsphaera*, *Podosphaera*.

ii. Perithecium

Perithecium (pl. perithecia, Gr. *peri* = around + *theka* = a case) is a flask -shaped ascocarp with a wall of its own. It is provided with a narrow ostiole and may possess a short or a long neck through which the asci are released at maturity. The asci are arranged in a regular manner and are lined the inside wall. The asci are intermingled with sterile filaments called *paraphyses*, which help the asci in with sterile filaments called *paraphyses*, which help the asci in nutrition and dispersal. The *paraphyses*, which are rigid and appear in the ostiole are called periphyses. The perithecia may be borne singly or in groups.



In Sphaeriales and Hypocreales, the perithecia are borne on or embedded in a mass of fungal tissue termed the 'perithecial stroma' and these are found in Xylariaceae and by *Cordyceps* and *Claviceps*. In some cases, in addition to the perithecial stroma, a fungus may develop a stromatic tissue on which or within which asexual spores or conidia develop. e.g. *Nectria cinnabarina* (Coral -spot fungus) forms pink conidial stromata. In perithecia, the ascus wall is

single and is called 'unitunicate' (L. *unus*=one+*tunica* =coat, mantle). Perithecia are produced by fungi in Hypocreales (*Hypocrea* , *Nectria*, *eratocystis*, *Podospora*, *Chaetomium*, *Xylaria*, *Ustulina*, *Rosellinia*, *Claviceps* and *Cordyceps*) in Sphaeriales.

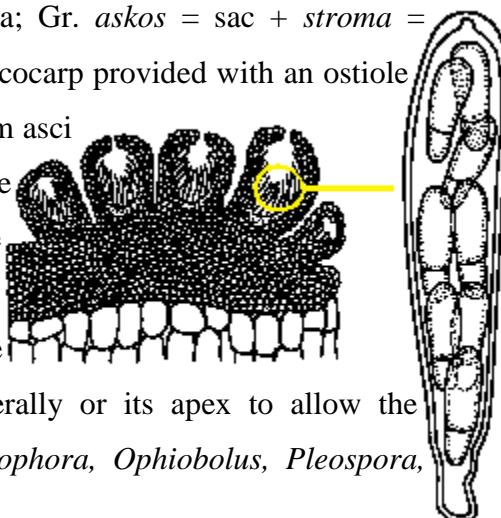
iii. Apothecium

Apothecium (pl. Apothecia; Gr. *apothekē*=store house) is an open ascocarp. It has a broad opening and is either cup or saucer shaped with asci arranged in a palisade layer within. It is usually fleshy or leathery in nature. An apothecium consists of three parts viz. hymenium, hypothecium and excipulum. The hymenium is the layer of asci that lines the surface of hollow part of the disc, cup or saddle. It is made up of club-shaped or cylindrical asci, usually with many or few paraphyses among them. These paraphyses may be as long as the asci, longer or somewhat shorter.

In some apothecia, the tips of paraphyses may be branched and the tips of branches may unite above the asci and form a layer called the epithecium (pl. epithecia; Gr. *epi* =upon+ *thēke* =a case). The 'hypothecium'(pl. hypothecia; Gr. *Hypo*=under+ *thēke* =a case) is a thin layer of interwoven hyphae, which is found immediately below the hymenium. The apothecium proper (i.e., the fleshy part of the ascocarp that supports the hypothecium and hymenium) is called excipulum (pl. excipula ; N.L. *excipulum*=receptacle), Excipulum consists of two parts viz., ectal excipulum and medullary excipulum. Ectal excipulum is the outer layer of the apothecium and the medullary excipulum is the inner portion. e.g. cup fungi (*Pyronema*, *Ascobolus*, *Peziza*, *Morchella* etc) in Pezizales and *Sclerotinia*, *Trichoscyphella* etc.) in elotiales.

iv. Pseudothecium

Pseudothecium or ascostroma (pl. ascostromata; Gr. *askos* = sac + *stroma* = mattress, cushion) like perithecium is a flask-shaped ascocarp provided with an ostiole through which the asci are discharged. In pseudothecium asci are directly formed in a cavity (locule) within the stroma. The stroma itself thus forms the wall of the ascocarp. In pseudothecium the ascus wall is double i.e. the ascus is bitunicate. The walls are separable. The outer wall does not stretch readily but ruptures laterally or its apex to allow the stretching of a inner layer. e.g. *Cochliobolus*, *Pyrenophora*, *Ophiobolus*, *Pleospora*, *Leptosphaeria* of the class Loculoascomycetes.



d. Basidiocarps

Basidiocarp (Gr. *basidion*=small base + *karps* = fruit) is a fruiting body, which bears basidia and basidiospores. Basidia are borne on the under surface of fruit body. Basidia bear basidiospores exogenously usually on projections called sterigmata. Basidia are typically formed in definite layers called hymenium (pl. hymenia; Gr. *hymen*=membrane). Hymenium is composed of basidia and large sterile structures called *cystidia* (sing. cystidium; Gr. *kystis* =bladder + *-idion* = dimin. Suffix). They are highly developed and have compound structure. Basidiocarps may be thin and crust-like, gelatinous, cartilaginous, papery, fleshy, spongy, corky or woody. They may vary in size from microscopic to a metre or more in dia. Most fungi in basidiomycotina except smuts (Ustilaginales) and rusts (Uredinales) form basidiocarps. They include mushrooms, (*Agaricus*, *Pleurotus*, *Volvariella*), shelf fungi, coral fungi (Clavariaceae) puff balls (Lycoperdaceae-*Lycoperdon* sp.) earth stars, (Gastraceae-*Gastrum* stinkhorns sp. (Phallales *-phallus*) and birds-nest fungi. (Nidulariales-*Nidula* sp.). The main body of the fungus in each case is the extensive mycelium, which usually goes unnoticed. Basidiocarp may be open from the beginning, exposing their basidia, or they may open at a later stage, or even remain closed. In closed basidiocarps the spores are liberated only on the disintegration of the basidiocarp or with its accidental fracture by external forces (e.g. *Lycoperdon*).

